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# THE AFFINITIES OF THE NEW ZEALAND PASSERINE GENUS *Turnagra*

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## ABSTRACT

The external structure, pterylosis, myology, and osteology of *Turnagra* show that this genus belongs in the bird-of-paradise/bowerbird assemblage and is not closely related to the Pachycephalinae. *Turnagra* appears to be the most primitive member of this assemblage, sharing similarities both with the paradisaeid subfamily Cnemophilinae and with the Ptilonorhynchidae.

## INTRODUCTION

In New Zealand exists (or existed, as the case may be) a singular passerine bird that up to the present has defied the attempts of taxonomists to find a comfortable place for it among the recognised families of oscines. The Maoris called it Piopio; ornithologists recognise it under the generic name *Turnagra*; and it has otherwise had the unfortunate sobriquet of "New Zealand thrush." There are two distinct forms of *Turnagra*: *capensis* of the South Island and adjacent islets and *tanagra* of the North Island. These have been regarded either as two distinct species or as races of a single species, *capensis*. In this paper the two forms are treated binomially; generalisations about "*Turnagra*" apply to both forms. Regrettably, both of these species are now apparently extinct (Mills & Williams 1979). Using study skins and the little anatomical material that was preserved, we undertook an investigation of *Turnagra* to determine its relationships among the large and diverse group of oscine passerines.

## TAXONOMIC HISTORY

Although originally described by Sparman (1787) as *Tanagra capensis*, no modern taxonomist has considered the species to belong to the New World family Thraupidae (tanagers); Linnaeus and his contemporaries used the generic name *Tanagra* for a world-wide miscellany of birds with similar bill shapes. The specific name *capensis* was based on the mistaken belief that the bird came from South Africa.

The genus *Turnagra* was proposed for *capensis* by Lesson in 1837. *Keropia* Gray, 1840, and *Otagon* Bonaparte, 1850, are junior synonyms encountered in the early literature. We shall attempt to

review here only the more important opinions concerning the placement of *Turnagra*, as in many of the early classifications the genus was associated with several different artificial groups of birds before family limits became somewhat stabilised.

As early as 1869, Buller put the North Island form of *Turnagra* under the family Turdidae (thrushes), although without stating his reasons at the time. Sundevall (1872), using rather dubious external characters (but perhaps to better effect than many of his successors), placed *Turnagra* in his family Ptilorhynchinae (*sic*), in which he included the bowerbirds *Ailuroedus*, *Ptilonorhynchus*, *Chlamydera*, and *Sericulus*, as well as the Australian genera *Struthidea*, currently placed in the Grallinidae, and *Cinclosoma*, a genus perhaps more problematical than *Turnagra* but not thought to be closely related to the Ptilonorhynchidae. Finsch (1872) had placed *Turnagra* in the Corvidae under the subfamily Glaucopinae (= the modern Callaeidae) but later (1874) transferred it to the Ptilonorhynchidae in deference to Sundevall. Although these actions had merit, as we shall see, this allocation of *Turnagra* was not generally adopted, probably because the whole of Sundevall's classification was soon discredited (see Newton, 1896: intro. 88-90).

To Buller and Hans Gadow we must credit most of the confusion concerning the relationships of *Turnagra*. In 1887 (p. 30) Buller wrote: "Mr. Sharpe has placed *Turnagra* among his Timeliidae; but I have decided to make it the type of a new family, Turnagridae, because the form seems to differ quite as much from typical *Timelia* as it does from *Turdus*." Buller went on to quote extensively from the anatomical notes supplied to him by Hans Gadow, whose conclusions were as follows:

After examination of the digestive apparatus, the pelvic nerve-plexus, the skeleton, and the pterylosis, I feel inclined to put *Turnagra* with the wide and ill-defined group of Timeliidae. *Turnagra* is certainly neither Corvine nor Fringilline, and it is in fact a member of the Southern (Indian Australian) mass of Thrush-like birds. Its bill and certain modifications of its digestive apparatus seem to show that this bird is a Thrush with **graminivorous propensities** [emphasis Gadow's]. I would put it into Sharpe's subfamily Ptilonorhynchidae, to which **AEluroedus** belongs, but unfortunately **Ptilonorhynchus** itself is very different from Timeliidae in its pterylosis.

Upon reading this passage, a modern ornithologist could hardly be faulted for having not the least idea of the true affinities of *Turnagra*, as no fewer than three currently recognised "families" of passerines are alluded to — Turdidae, Timaliidae, and Ptilonorhynchidae. Even today, the "family" Timaliidae is regarded as a poorly defined group, and in Sharpe's time it was an even more heterogeneous conglomeration, being described as a "refuge for the destitute" containing a great many forms that "cannot . . . be conveniently stowed elsewhere" (Newton 1896: 25). Despite the am-

biguity of Gadow's conclusion, it was doubtless his continued allusion to thrushes that kept the Turdidae under consideration for so long. This is but another of many examples of how uncritical acceptance of Gadow's preliminary examinations became fixed in the literature for generations (as with *Pedionomus*, for example — Olson & Steadman 1981).

Buller's writing (1887) further associated *Turnagra* with the word "thrush" and at the same time influenced subsequent classifiers to regard *Turnagra* as forming a monotypic family, an action that did little to elucidate the relationships of the genus. Oliver (1930) originally adopted the use of Turnagridae and cited the above quotation from Gadow (in Buller 1887), but later he showed that the palate of *Turnagra* was not similar to that of *Turdus* and recommended that *Turnagra* "be placed in the neighbourhood of *Gymnorhina* [Cracticidae]" (Oliver 1945: 148).

Mayr & Amadon (1951: 20) stated that *Turnagra* probably belonged in the Pachycephalinae rather than in the Turdinae, citing Oliver's observation that the skull is very different from that of *Turdus*, but without giving reasons for allying the genus with *Pachycephala* and its presumed relatives. Oliver (1955: 524) countered Mayr & Amadon, stating that the palate of *Turnagra*

. . . differs essentially from that of the true thrushes, and also from that of the thickheads (*Pachycephala*) with which *Turnagra* has recently been allied. The maxillo-palatines meet in front of the vomer as they do in the Australian Magpie (*Gymnorhina*) and the Manucode (*Manucodia*). Accordingly I have removed the family Turnagridae from the neighbourhood of the thrushes. . . . Finsch placed *Turnagra* with the bower birds, a much better position than with the thrushes.

Finsch's arrangement, as we have seen, is properly attributed to Sundevall.

On the basis of Oliver's work, the OSNZ Checklist Committee (1953: 68) retained *Turnagra* "in a separate family, near the Cracticidae (Bell Magpies) and Ptilonorhynchidae (Bower Birds)" and this treatment was followed in the subsequent edition (1970). Mayr (1967: 52) placed *Turnagra* as a genus *incertae sedis* after the Pachycephalinae, noting that it was "of uncertain affinity but more similar to the whistlers than to the thrushes where the genus is often placed." Ames (1975: 127) briefly reviewed the taxonomic history of *Turnagra*, concluding that it "is now usually regarded as [a] non-thrush of uncertain affinities." He observed that the generalised oscine syrinx of *Turnagra* is unlike the diagnostically specialised syrinx of the Turnidae.

Our study was initiated in 1975, when Olson, who was familiar with specimens of *Turnagra capensis*, first chanced to examine skins of the Tooth-billed Bowerbird (*Scenopoeetes dentirostris*). He was immediately struck by the great resemblance in colour and pattern of these two species. This sparked our collaborative effort and we pre-



FIGURE 1 — Ventral view of study skins of *Turnagra capensis* (left) and the Tooth-billed Bowerbird, *Scenopoeetes dentirotis*, to show the great similarity in plumage pattern

sented our conclusions at a meeting later in the same year (American Ornithologists' Union, Winnipeg). Since then, both Fleming (1982) and Sibson (1982) have mentioned a possible connection between *Turnagra* and the bowerbirds, particularly *Scenopoeetes*, citing behavioural as well as external morphological evidence. Fleming's suggestion, and probably Sibson's as well, stems from unpublished observations of D. H. Brathwaite and K. A. Hindwood dating back to 1968.

That our discovery of similarities between *Turnagra* and *Scenopoeetes* was completely independent is testimony to the strength of the resemblances between these two genera.

The present paper attempts to support the hypothesis of relationship between *Turnagra* and the bowerbird group on the basis of different aspects of morphology. Parkes, who had already become interested in variation within *Turnagra* (Parkes, MS), undertook the comparisons of external morphology. Clench, who had made detailed studies of the pterylosis of bowerbirds in another connection, provided a comparison of the pterylosis of *Turnagra* with that of several of the suggested relatives of the genus. Borecky's PhD dissertation at the University of Pittsburgh (1977) deals with the appendicular myology and relationships of the so-called "corvid assemblage." In the course of his investigations, he was able to dissect a specimen of *Turnagra* to determine whether appendicular myology could throw any light on the relationships of the genus. Olson is responsible for the osteological comparisons, the taxonomic history, and the final organisation and preparation of the manuscript.

#### EXTERNAL CHARACTERS

We have alluded above to the striking general resemblance in plumage pattern between *Turnagra capensis* and *Scenopoeetes denti-rostris* (Fig. 1). General proportions of the two are also quite similar. We also noted the following additional similarities in epidermal structures: tarsal scutellation; wing formula; relative development of chin, rictal, and nasal bristles; and a series of slight grooves anterior to the nostrils in most specimens. The yellow eye has also been cited as resembling bowerbirds of the genera *Sericulus* and *Prionodura* (Fleming 1982).

The heavy toothed bill of *Scenopoeetes* differs markedly from the relatively unspecialised bill of *Turnagra*, but likewise from that of all other bowerbirds. The bill of *Turnagra*, on the other hand, is very similar to that of bowerbirds such as *Amblyornis* (Fig. 2). The tail of *Turnagra* is proportionately longer than that of *Scenopoeetes* but no more so than in *Chlamydera* or *Prionodura*. In both *Turnagra* and *Scenopoeetes* the two outermost primaries (P-10, P-9) are straight edged; *Turnagra* then has the next three primaries, and *Scenopoeetes* the next four primaries, with sinuated outer webs.

Only two specimens in the AMNH series of *Scenopoeetes* have remnants of an "immature" plumage. These plumage remnants show characters resembling *Turnagra capensis* as follows: dark barring or edging of under tail-coverts fainter or lacking in immatures; the upper wing-coverts that are broadly rufous-edged in *T. capensis* are narrowly edged with pale rufous (specimens worn and faded) in *Scenopoeetes* (wholly lacking in adults); in what appears to be the younger specimen of *Scenopoeetes* (AMNH 697435) the ear coverts are somewhat more rufescent, less dark olive-brown than in adults, recalling the more rufous face of most young *Turnagra capensis*.



FIGURE 2 — Lateral view of study skins of the Tooth-billed Bowerbird, *Scenopoeetes dentirostris* (top), *Turnagra capensis* (middle), and a more typical bowerbird, *Amblyornis macgregoriae* (bottom). Whereas the heavy bill of *Scenopoeetes* is distinctive, the bill of *Turnagra* is similar to that found in other bowerbirds.

One of the most interesting similarities between *Turnagra* and bowerbirds is the fairly frequent occurrence of asymmetrical central rectrices. In *Turnagra capensis* AMNH 591959, for example, both central rectrices are fresh and unsheathed; R-1 is about 5.5 mm longer than L-1. It should be stressed that *all* of these rectrices are of "adult" shape; in *Turnagra*, "immature" rectrices are longer, and narrower, than "adult" rectrices (Parkes, MS). In one of the two apparent first-year specimens of *Scenopoeetes* (AMNH 679435), R-1 is about 13 mm shorter than L-1, with no evidence (basal sheathing) of continuing growth. In a presumed adult (AMNH 679422), R-1 is about 3.5 mm shorter than L-1. This phenomenon occurs in other bowerbirds as well. In three adult males of *Amblyornis macgregoriae mayri* (AMNH 679533, 679529, 342276), R-1 is about 8 mm, 3.5 mm, and 5.5 mm shorter than L-1, respectively, with no sheathing at the base of the shorter rectrix. An adult male of *Archboldia papuensis sanfordi* (AMNH 705705) shows R-1 about 8 mm shorter than L-1, again with no sheathing at the base.

The significance of the occasional appearance of asymmetrical central rectrices in *Turnagra* and bowerbirds is not clear, but that it may indicate relationship is suggested by examination of the 101 specimens of Pachycephalinae in the Carnegie Museum, none of which shows more than 1 mm difference in length between R-1 and L-1.

#### COMPARATIVE PTERYLOSIS OF *TURNAGRA*

Unfortunately, the study of the body pterylosis (feather tracts) of *Turnagra* is hampered by the lack of adequate material. The only two known spirit specimens are both badly damaged by shot and one is in heavy moult. We probably should not complain, however, for like most rare and interesting birds, if they had not been poor specimens when collected they undoubtedly would have been made into study skins rather than anatomical specimens. It is also unfortunate that a spirit specimen of *Scenopoeetes* does not exist, although we were able to study the gross aspects of its pterylosis in an unstuffed study skin at the AMNH.

The general body pterylosis of *Turnagra* is clearly more similar to the kinds of patterns and density of feathering found in members of the bird-of-paradise/bowerbird assemblage than to those of the Muscicapidae (*sensu lato*) or other oscines. The dorsal tract exhibits most of the taxonomically interesting variation and in *Turnagra* is very heavily feathered, with an exceptionally dense saddle composed of approximately 15 rows containing a total of about 300-327 feathers (2 specimens). No saddle apterium is apparent, but the condition of both specimens does not preclude the possibility of a very small apterium at the posterior end of the element. The ventral tract is also heavily feathered and of typically oscine configuration.

In contrast, the saddles of thrushes are much more lightly feathered, averaging about half as many feathers (counts of 141-184



in nine or ten rows: 8 specimens of 5 species of 3 genera, including *Turdus*). A specimen of *Pachycephala flavifrons* (Pachycephalinae) was found to have a typically oscine saddle of 117 feathers in nine rows. A poor specimen of *Lamprolia victoriae* also had a typically oscine saddle, with nine or ten rows and no apterium; overall it was very like *Pachycephala* and *Muscicapa*. Although the saddles of corvids are of a different pattern, they are relatively lightly feathered, with counts ranging from 50 in six rows for *Platylophus*, to 198 in 12 rows for a Common Raven (*Corvus corax*); 15 other genera are intermediate in number (114-178). Nor do the Cracticidae or Grallinidae have notably heavy saddles. One specimen of *Cracticus* has 10 saddle rows, and *Grallina* and *Struthidea* have 9, versus 15 in *Turnagra*. Two specimens of Callaeidae (*Heterolocha* and *Callaeas*) both have saddles containing 298 feathers in 14 rows, which is comparable to *Turnagra*'s 300-327 in 15. Pattern differences in the saddle, and especially in the ventral tract, however, argue against a close relationship between *Turnagra* and the Callaeidae.

Within the bird-of-paradise/bowerbird complex, several patterns and degrees of feathering occur. Of the bowerbirds available as fresh or spirit specimens (*Ailuroedus*, *Amblyornis*, *Sericulus*, *Ptilonorhynchus*, and *Chlamydera*), all have heavy saddles, with 180-281 feathers, ranging from 11 to 15 rows long; the single study skin of *Scenopoeetes* also has a heavily feathered saddle. The pattern of bowerbird saddles differs from that of most oscines, however, in that a long and conspicuous apterium is present at the base; *Scenopoeetes* has such an apterium. Saddle apteria of various sizes also occur in almost all corvids, and in *Grallina* (but not in *Struthidea* or *Corcorax*), in some cracids, and a few other oscines (Clench, MS).

The birds-of-paradise show a strong dichotomy in both dorsal and ventral tracts. The "typical" genera (subfamily Paradisaeinae, of which we have examined 14 of 17 genera as fresh or spirit specimens) have strikingly sparse feathering. Saddles range from 7 to 10 rows in length, with 83-180 feathers; *Astrapia* differs somewhat with 200 or 201 feathers in 11 rows. Typical birds-of-paradise also have a distinctive and characteristic pattern at the base of the saddle — a wide spacing of the central feathers, giving the appearance of a small apterium. *Astrapia* is similar, but it also lacks the central feather of the posterior-most row and hence has a true, if very small, apterium.

Of the other subfamily of paradisaeids (Cnemophilinae), which Bock (1963) considered to represent the ancestral stock of both the Paradisaeinae and the Ptilonorhynchidae, we have examined all three genera — *Loria* in detail and *Cnemophilus* and *Loboparadisaea* in poor specimens. *Loria* exhibits a strong contrast to the typical birds-of-paradise in that it has a long and heavy saddle — 225-254 feathers in 13 rows (two specimens). *Cnemophilus* and *Loboparadisaea* are similarly heavily feathered. None has the posterior saddle "weakness" characteristic of the Paradisaeinae. On the contrary, the cnemophilines show a definite pterylographic similarity to *Turnagra*.

In summary, with the comparative material at present available, the pterylosis of *Turnagra* strongly suggests that this genus belongs in the bird-of-paradise/bowerbird assemblage rather than in the Muscicapidae (*sensu lato*). Within this assemblage it is most closely similar to the members of the Cnemophilinae.

#### MYOLOGY

In his study of the so-called "corvid assemblage," Borecky (1977) compared the appendicular myology of *Turnagra capensis* with that of representatives of five genera of Ptilonorhynchidae (*Ailuroedus*, *Amblyornis*, *Sericulus*, *Ptilonorhynchus*, and *Chlamydera*) and nine genera of Paradisaeidae (*Loria*, *Manucodia*, *Semioptera*, *Epimachus*, *Astrapia*, *Parotia*, *Cicinnurus*, *Diphyllodes*, and *Paradisaea*). Because Mayr (1967) placed *Turnagra* near the Pachycephalinae, the hindlimb myology of *Pachycephala* and *Hylocitrea* was also examined for the present study.

In *Pachycephala* and *Hylocitrea*, *M. obturatorius lateralis* pars dorsalis is relatively small and has a fleshy insertion on the tendon of *M. obturatorius medialis* and the head of the femur. This is the

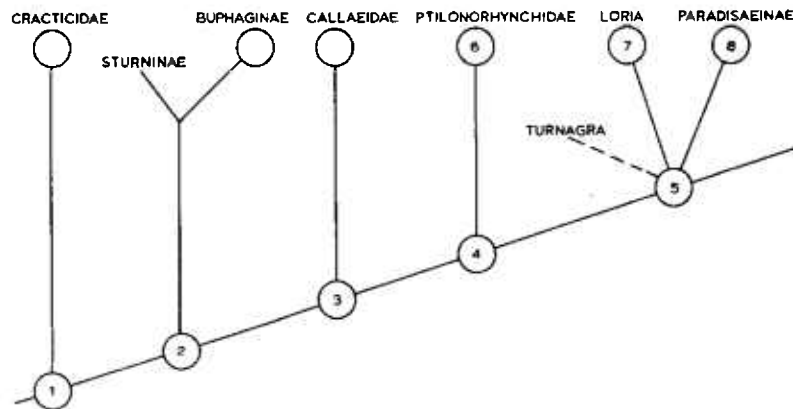


FIGURE 3 — Phylogenetic affinities as proposed by Borecky (1977) on the basis of myology (modified so as to omit characters not pertinent to the present discussion). (1) *M. obturatorius lateralis* pars dorsalis relatively large and inserting tendinously on the femur; (2) *M. flexor perforatus* digiti II is not perforated by the tendon of *M. flexor digitorum longus*; (3) *M. iliofemoralis externus* present (Type 1); (4) *M. flexor hallucis brevis* large; (5) Type 2 *M. iliofemoralis externus* present and reversal of *M. flexor perforatus* digiti II to the bifurcate and perforate condition; (6) *M. deltoideus minor* arising from the scapula and coracoid; (7) *M. deltoideus minor* arising from the scapula and coracoid; (8) Type 3 *M. iliofemoralis externus* present and femoral head of origin of *M. flexor digitorum longus* present.

primitive condition. In *Turnagra*, the Paradisaeidae, Ptilonorhynchidae and certain other families, *M. obturatorius lateralis pars dorsalis* is relatively large and inserts by means of a tendon on the head of the femur just cranial to the insertion of *M. obturatorius medialis* (character 1 in Fig. 3). *Pachycephala* and *Hylocitrea* lack *M. iliofemoralis externus*, which is present in *Turnagra*, the Callaeidae, Ptilonorhynchidae, and Paradisaeidae (character 3 in Fig. 3). The presence of this muscle in passerine birds represents a derived character state (Borecky 1977). *Turnagra* shares no derived myological features with the two members of the Pachycephalinae examined and therefore it should not be included in that group.

Because *Turnagra* possesses the Type 2 configuration of *M. iliofemoralis externus*, a trait otherwise observed only in *Loria*, Borecky (1977) provisionally placed *Turnagra* near the Paradisaeidae (Fig. 3). This, however, is in conflict with the fact that *Turnagra* lacks an enlarged *M. flexor hallucis brevis*, a derived condition shared by the Ptilonorhynchidae and Paradisaeidae (character 4 in Fig. 3). In *Turnagra*, *Ailuroedus*, and *Chlamydera* (Ptilonorhynchidae), the tendon

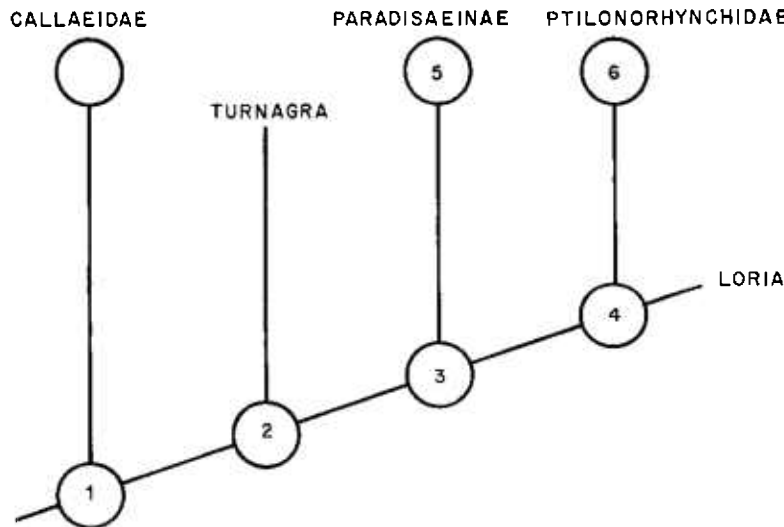


FIGURE 4 — Alternative phylogeny using the same myological characters as Borecky (1977). (1) Type 1 *M. iliofemoralis externus* present; (2) Type 2 *M. iliofemoralis externus* present; (3) *M. flexor hallucis brevis* large and reversal of *M. flexor perforatus digiti II* to the bifurcate and perforate condition; (4) *M. deltoideus minor* arising from the scapula and coracoid; (5) Type 3 *M. iliofemoralis externus* present and femoral head of origin of *M. flexor digitorum longus* present; (6) reappearance of Type 1 *M. iliofemoralis externus*.

of insertion of *M. flexor perforatus digiti II* is not perforated by the tendon of *M. flexor digitorum longus*. This is a derived condition (character 2 in Fig. 3) that is assumed to have reversed to the primitive state in the Paradisaeidae (part of character suite 5 in Fig. 3), but because such a reversal must also be postulated for the remainder of the Ptilonorhynchidae as well as two of the three species of Grallinidae (Table 4 in Borecky 1977), the significance of this character is doubtful. *M. flexor perforans et perforatus digiti II* in *Turnagra* and *Ailuroedus* does not ensheath the tendon of *M. flexor digitorum longus*, which is a derived condition suggesting that *Turnagra* may be allied to the bowerbirds.

An alternative phylogeny can be suggested from the same characters (Fig. 4). In this, *Turnagra* would branch off before the Paradisaeidae and Ptilonorhynchidae to reflect the fact that it does not have an enlarged *M. flexor hallucis brevis* (part of character suite 3 in Fig. 4). With the arrangement proposed here, the derived condition of *M. deltoideus minor* would define the Cnemophilinae and Ptilonorhynchidae as a monophyletic group (character 4 in Fig. 4), instead of evolving independently in these lineages (characters 6 and 7, which are the same, in Fig. 3). This has the disadvantage of requiring the Type 1 condition of *M. iliofemoralis externus* to reappear in the Ptilonorhynchidae. This is conceivable, however, as such a reappearance presumably also took place in the Paradisaeinae, where *Epimachus* has the Type 1 condition and the other species have Type 3.

Each of the phylogenies proposed on the basis of myology requires several reversals or reappearances of characters. Although that in Fig. 4 may require fewer, neither is entirely satisfactory, suggesting that these few variable myological characters may be inadequate for resolving branching sequences within the bird-of-paradise/bowerbird assemblage, particularly in the absence of myological information on members of the Cnemophilinae other than *Loria* and of ptilonorhynchids such as *Scenopoetes*.

Although the appendicular myology of *Turnagra* strongly suggests that it is a member of the bird-of-paradise/bowerbird assemblage, it does not clearly indicate that *Turnagra* belongs with either the Ptilonorhynchidae or the Paradisaeidae, as presently defined. If the Type 2 *M. iliofemoralis externus* is a derived character state within this assemblage, this would suggest that *Turnagra* is closely allied to the Cnemophilinae, as exemplified by *Loria*. On the other hand, the patterns of insertion of *M. flexor perforatus digiti II* and *M. flexor perforans et perforatus digiti II* might suggest that it is more closely allied to some members of the Ptilonorhynchidae.

#### OSTEOLOGY

Our osteological studies included three unsexed skeletons of *Turnagra*, none of which has data or is certainly identified as being one or the other of the two forms of the genus. These specimens are

TABLE 1 — Measurements of the three known skeletons of *Turnagra*. Because of its larger size and characters of the bill, the NMNZ specimen is presumed to be *T. tanagra* and the other two are presumed to be *T. capensis*. \* = damaged.

	NMNZ 15080	MCZ 1349	ANSP 38708
Total length of skull	50.9	47.2	45.5
Length of bill from naso-frontal hinge	25.1	22.4	21.8
Width of cranium at postorbital processes	23.3	20.6	----
Width of bill at posterior margin of nostrils	12.6	11.0	10.2
Length of mandible	38.0	34.2	33.9
Length of mandibular symphysis	11*	10.0	9.2
Width of mandibular symphysis at posterior margin	9.2	7.5	7.2
Length of sternal carina	29.6	26.9	27.0
Width of sternum at articulation of last rib	16.2	14.9	14.6
Length of ilium	30.8	30.0	28.8
Width of pelvis across antitrochanters	22.1	21.8	----
Length of coracoid	27.7	24.7	24.0
Length of humerus	33.0	----	31.0
Length of ulna	35.8	----	33.4
Length of carpometacarpus	19.7	----	17.5
Length of femur	33.2*	32.9	----
Length of tibiotarsus	55.3	51.8	----
Length of tarsometatarsus	40.1	36.8	----

as follows: National Museum of New Zealand 15080, Museum of Comparative Zoology 1349, and Academy of Natural Sciences of Philadelphia 38708 (lacking both hindlimbs).

The NMNZ specimen differs considerably from the other two in size (Table 1) and in the following skull characters: (1) all portions of the palatines wider; (2) posterior portion of palatines rounded, without transpalatine processes (possibly broken, but if so this was not evident under magnification and furthermore the right and left palatines are identical to each other); (3) pterygoids noticeably wider; (4) zygomatic process thicker; (5) lacrimo-ectethmoid complex much more inflated; (6) bill deeper, appearing proportionately shorter; (7) internarial bar more robust. The larger size and more robust bill of this specimen suggests that it may be *Turnagra tanagra*, the North Island form, whereas the other two may be *Turnagra capensis*. The differences between the putative specimen of *tanagra* and the other two are considerable and, if constant, would certainly suggest that the two forms of *Turnagra* are specifically distinct.

The overall morphology of the skull of *Turnagra* is quite similar to that of bowerbirds such as *Ailuroedus* (Fig. 5). This applies to bill shape, proportions, and architecture of the palate. In the two smaller specimens that are probably *T. capensis*, there are well-developed transpalatine processes exactly resembling those of *Ailuroedus*. Such transpalatine processes were considered by Bock (1963) to be characteristic of bowerbirds, at least within the bird-of-paradise/bowerbird assemblage. In the one skull of *Scenopoeetes* that was available for this study, however, the transpalatine processes are absent and the posterior margins of the palatines are rounded, with a somewhat serrated edge (Fig. 6). The palatines in the skeleton of *Turnagra* cf. *tanagra* (Fig. 6) are like those of *Scenopoeetes* and quite different from the palatines in the other two specimens of *Turnagra* or of other bowerbirds. The significance of these differences is difficult to assess.

On the basis of osteology, plumage, and behaviour as described by Gilliard (1969), we see little justification for the recent trend towards submerging *Scenopoeetes* in *Ailuroedus*, as has been done in several recent Australian publications. *Scenopoeetes* appears to be quite distinct, and it is not particularly evident that *Ailuroedus* is necessarily closely related to it.

*Turnagra* differs from all bowerbirds in lacking large, free lacrimals and in having the zygomatic process better developed. In both these respects, however, *Turnagra* resembles the paradisacid subfamily Cnemophilinae (*Macgregoria* only for the zygomatic — see Bock 1963). *Turnagra* appears to differ from the other taxa examined in having the maxillopalatines poorly ossified, being rather amorphous structures that are not easily separable from the surrounding cartilage.

The presence of a well-developed lacrimal bone in the Ptilonorhynchidae would seemingly be the primitive condition, whereas its

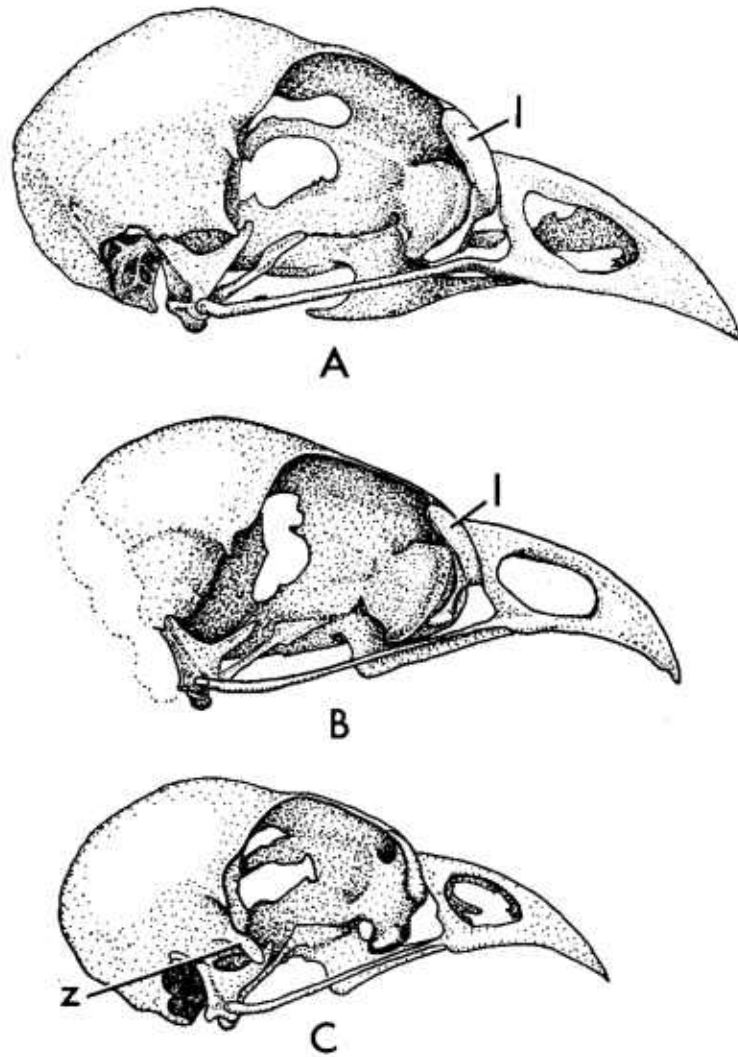


FIGURE 5 — Lateral view of the skull of (A) Green Catbird, *Ailuroedus crassirostris* (Ptilonorhynchidae); (B) Tooth-billed Bowerbird, *Scenopoeetes dentiostrius* (Ptilonorhynchidae); (C) *Turnagra* sp. (the NMNZ specimen presumed to be *T. tanagra*). Although the skull of *Turnagra* is generally similar to that of bowerbirds, note the absence of the lacrimal (l) and the well-developed zygomatic process (z) of *Turnagra*, both of which characters are found in the Cnemophilinae.

loss would be derived. Bock's (1963) proposed phylogeny and that in Fig. 4 would require the evolutionary reappearance of this bone, which considering how many different myological traits must have reappeared, no matter how the various bowerbirds and birds-of-paradise are arranged, cannot flatly be ruled out. On the other hand, it does appear that in other passerines (e.g. Rhinocryptidae) the lacrimal may be incorporated into the ectethmoid and eventually obliterated (Feduccia & Olson 1982). Thus, it is not possible at this point to say whether the absence of a lacrimal in *Turnagra* is primitive or derived. In overall similarity, *Turnagra* would have to be said to resemble the Cnemophilinae more than the Ptilonorhynchidae in this respect.

The Pachycephalinae was included in the comparisons because of Mayr's (1967) placement of *Turnagra* near that group. The skull of *Turnagra* agrees with that of the bowerbirds and differs from *Pachycephala* as follows: (1) rostrum much heavier and more decurved; (2) premaxillary symphysis longer; (3) nasal bar stouter; (4) partially ossified nasal septum present; (5) ventral surface of premaxillary symphysis more excavated, with a distinct median ridge; (6) nostril relatively shorter and deeper; (7) orbital process of quadrate much longer. The skull of *Turnagra* therefore does not suggest a close affinity with *Pachycephala*. On the other hand, it shows considerable similarity to the Ptilonorhynchidae and the Cnemophilinae, and nothing in its structure would preclude *Turnagra* from being associated with the bird-of-paradise/bowerbird assemblage.

#### CONCLUSIONS

Derived characters of myology and pterylosis indicate that *Turnagra* belongs in the bird-of-paradise/bowerbird assemblage. The osteology, external morphology, and plumage characters of *Turnagra* are compatible with this placement, whereas we found no anatomical or plumage characters that would support a relationship between *Turnagra* and the Pachycephalinae.

The greatest remaining difficulty is deciding where *Turnagra* best fits within the bird-of-paradise/bowerbird assemblage, as there is considerable conflict among the various characters. In the pterylosis and some myological and osteological characters, the greatest similarity is to the Cnemophilinae. In plumage pattern, overall external appearance, and in other osteological and myological characters there is greater similarity between *Turnagra* and the Ptilonorhynchidae. *Turnagra* has none of the derived characters that define the Paradisaeinae and it may be safely assumed that the genus does not belong in that subfamily.

The small *M. flexor hallucis brevis* and rather generalised overall structure suggest that *Turnagra* may be the most primitive member of the bird-of-paradise/bowerbird assemblage and thus closest to the common ancestor of that group. This might help to explain the conflicting nature of many of its characters, *Turnagra* possibly



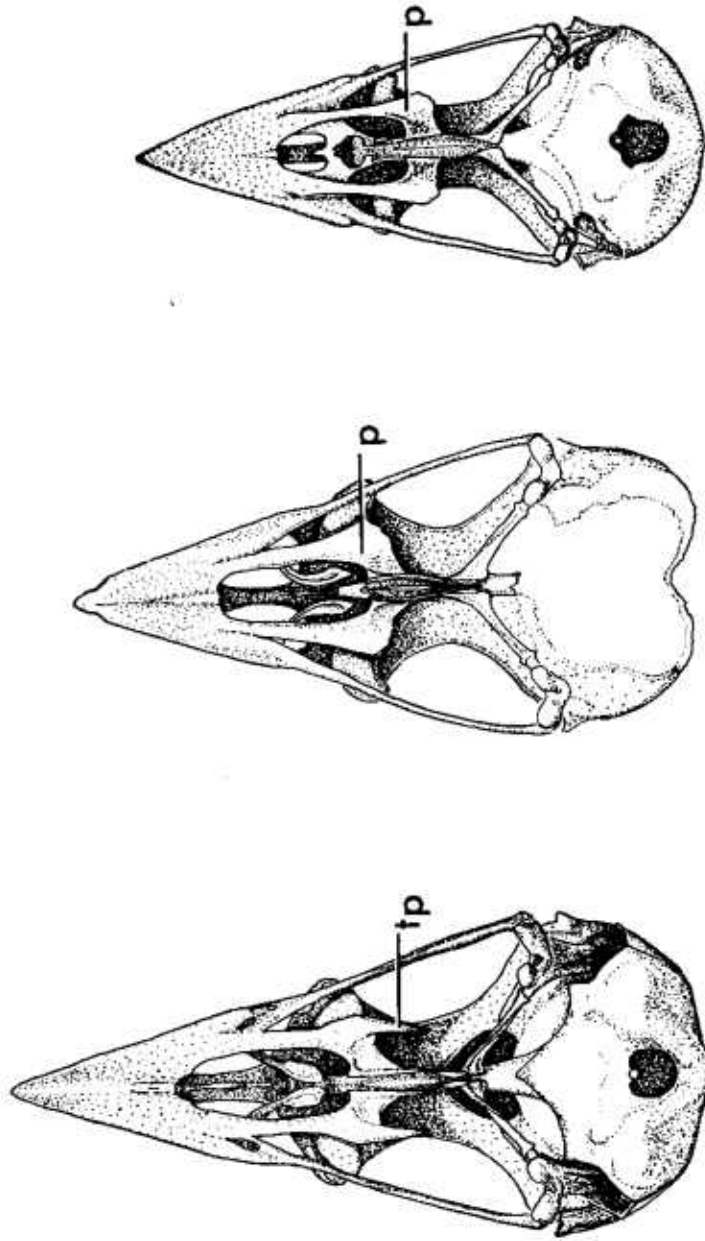


FIGURE 6 — Ventral view of skulls of (A) Green Catbird, *Ailuroedus crassirostris* (Ptilonorhynchidae); (B) Tooth-billed Bowerbird, *Scenopoeetes dentirostris* (Ptilonorhynchidae); (C) Turnagra sp. (the NMNZ specimen presumed to be *T. tanagra*). Although the shape of the palatines (p) in *T. tanagra* is similar to that in *Scenopoeetes*, in the two skeletal specimens examined that are presumed to be *T. capensis* the transpalatine processes (tp) were well developed as in typical bowerbirds.

having branched off before the other groups evolved many of their distinctive features.

What, then, do we do with *Turnagra* taxonomically? We shall begin with the premise that monotypic families of passerines are highly undesirable. Maintaining a separate family Turnagridae cannot be justified on anatomical grounds because there are no derived characters by which such a family could be defined that are not found in some other member of the bird-of-paradise/bowerbird assemblage. Furthermore, this would do nothing to clarify the relationships of the bird. Until the branching pattern within the bird-of-paradise/bowerbird assemblage can be worked out in better detail, it seems best to place all members of this assemblage in a single family, Paradisaeidae, with the Ptilonorhynchidae being reduced to a subfamily. Within this expanded family, *Turnagra* should be placed first, either without assigning it to a particular subfamily or maintaining it for the present as a separate subfamily, Turnagrinae. In addition, we applaud the current use by New Zealand ornithologists of the vernacular name Piopio and strongly recommend that the word "thrush" no longer be used for *Turnagra*.

As a member of the Paradisaeidae, in the broad sense, *Turnagra* demonstrates once again the intimate connection between the avifauna of New Zealand and that of Australia and New Guinea. It is of interest that there has been essentially no radiation of these birds in New Zealand, there being only two forms of *Turnagra*, which from their osteology appear to be distinct species.

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